BREEDING BIOLOGY OF THE LEAST BITTERN

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The Least Bittern (*Ixobrychus exilis*) is one of the most inconspicuous of all marsh birds. It is neither shy nor rare within its range but is merely a quiet bird which lives out of sight among marsh emergents. Observations on the species have been numerous but brief, and no detailed study of any phase of its breeding biology has been published. However, considerable data have been reported on the closely related Little Bittern (*I. minutus*) of Eurasia. The data presented here were obtained during 1958–1960 at Goose and Little Wall lakes near Jewell, Iowa, and at Trumbull and Rush lakes near Ruthven, Iowa.

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GENERAL HABITS

Of the two North American bitterns, the Least Bittern leads a more over-water existence than does the American Bittern (*Botaurus lentiginosus*). The American Bittern usually is a shore-line wader which nests in edge emergents with the nest resting on the ground (Abbott, 1907; Vesall, 1940; and present study). The Least Bittern spends its time over deeper water where it uses emergent vegetation as "stepping-stones." It feeds on the open-water side of the emergents by clinging to the vegetation and extending its long neck (Eastwood, 1932; Sutton, 1936). Saunders (1926) reported that these small herons rarely missed their target and were constantly on the move when hunting. When alarmed, they assume the "freezing" action so characteristic of the group (Palmer, 1909; Allen, 1915), and when approached they take flight with legs dangling.

NEST SITES

Nesting usually occurs in emergent vegetation several feet in height. Of 89 nests found during the present study (Table 1), 50 nests found by Trautman (1940), and 30 nests found by Beecher (1942), most were in *Typha*, *Carex*, *Scirpus*, and plants of similar physiognomy. Occasionally, nests are found in *Phragmites* (Bent, 1926; Dillon, 1959), *Sagittaria* (Potter, 1917), and *Salix* or *Cephalanthus* stems in water (Bales, 1911; Baker, 1940; Potter, 1917; Trautman, 1940). One nest found by Provost (1947) was supported by barbed wire. A nest on the ground in weeds was reported by Roberts (1936: 192) and nests on bog or drift were found by Cooke (1881), Chapman

Table 1

Nesting Cover Observed During Present Study

Vegetation	No. nests
Typha spp.	13
Typha-Scirpus acutus	23
Typha-Scirpus fluviatilis	2
Typha-Salix	1
Scirpus acutus	14
Scirpus fluviatilis and *S. acutus*	11
Scirpus fluviatilis	15
Carex spp.	3
Phragmites communis	2
Mixture of any three above	5
Total	89

(1900), and Abbott (1907). Nests in *Salix* or Mangrove (*Rhizophora*) over ground were noted by Trautman (1940) and Howell (1932), respectively. Old nests of a Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and a White-crowned Pigeon (*Columba leucocephala*) were reported as bases for bittern nests by Roberts (1936) and Beatty (1943).

A natural clump of vegetation of the previous year usually forms the foundation for the nest. The importance of this old vegetation was shown by changes in the distribution of nests at Goose Lake in central Iowa. During 1958, considerable emergent vegetation remained in the center of the marsh after winter. The five nests found were in this cover. During the spring of 1959, a water level increase caused the loss of most of the old vegetation so that little cover existed in the center of the marsh when nesting started. All seven nests found during 1959 were in the edge vegetation, and although new and dense vegetation developed in the marsh center by the time of the second nestings, no nests were found there. These central emergents were used for feeding, however.

The nest base also is formed by bending down of new and old vegetation, and then short stems are added on top. Potter (1917) reported that "sticks" brought to a nest site among *Sagittaria* were laid in a criss-cross pattern like the spokes of a wheel (Fig. 1). Wackernagel (1950) made a similar generalization for the nest of the Little Bittern. The platform usually consists of the same species of vegetation as the base, but it may differ when floating debris is used. However, material rarely is carried more than a few feet. Bent (1926:85) mentions a nest built in "rushes" and constructed entirely of "sticks." A similar nest found during this study was constructed of willow

Fig. 1. Nest in hardstem bulrush at Goose Lake, Iowa, showing criss-cross pattern of nest material.

sticks, but they had been gathered from within a few feet of the nest and placed in some isolated stalks of cat-tail.

The size of the nest probably varies with the type of vegetation and the particular clump selected for the nest, but most nests are 5 to 8 inches in diameter. Bent (1904) gave measurements of two nests as 4 × 7 and 5 × 7 inches, presumably the dimensions being width and length. Simmons (1915) reported a nest 6½ inches across, and Baker (1940) found one 8 inches in diameter. A nest located by Pearson (1909) was 4 inches deep and 9 inches across.

Nests normally are placed from six up to 24 inches above water but often sink to water level from the combined weight of young and adults. Nests were found in water three to 38 inches deep; nests over land (Saunders, 1926; Roberts, 1936; Trautman, 1940) probably result from water level declines. That water conditions are important to nesting populations was shown by water level changes in Rush and Trumbull lakes in northwestern Iowa. Bitterns were common at both lakes during 1958; four nests were found in a small area of one lake and adults were seen regularly. Only one nest was found at the other lake because no intensive nest hunting was done, but the abundance of young seen in late summer indicated that numerous birds were present. In mid-May of 1959, when bitterns arrived in Iowa, water levels at both of the lakes were so low that there was little water at the base of emergent vegetation. Despite the fact that field work in the area was more intensive during 1959 than 1958, only one adult was seen at each lake and no nests or young were found.

Nests are usually located adjacent to a patch of open water, as observed not only in this study but by Cooke (1881), Simmons (1915), Saunders (1926), and Nero (1950). Of 87 nests observed for this feature in Iowa, all were 6 inches to 20 feet (averaged about 8 feet) from open water of lakes, channels, or openings made by muskrats.

PRE-LAYING ACTIVITIES

Evidence for territoriality in bitterns is limited. Kent (1951) found that nests were evenly spaced in a small lake, and observations during my study substantiate this conclusion. Relative concentrations probably develop in particularly suitable habitat. Kent (1951) found 19 nests in a 44-acre marsh, and Beecher (1942) found one nest per four acres of usable vegetation. Wood's observation (1951) of 15 nests in two acres of vegetation is exceptional. During the present study, 62 nests were found in the 83-acre Goose Lake during 1960, but some of these probably represent renests or second nests. Several cases were noted of two active nests only 15–20 feet apart. Only one observation suggests territorial behavior: Davidson (1944) saw a paired male assume a hump-shouldered defensive attitude before an intruding male. This conflict ended in the retreat of the intruder.

Nest-building seems to be performed mostly by the male. Davidson (1944) noted that at a single nest the male did most of the building although the female was present. He brought material for the female when she was on the nest. Other nest-building behavior observed later in incubation (see below) also implies that males do most of the building.

During the present study, only one nest was found prior to laying; this nest essentially was complete seven days before laying. The presence of a blind may have influenced this delay, but there is also the possibility that the nest is used as a site for courtship and copulation. No courtship display has been observed, but a "cooing" call has been described by several authors. I have never heard any such sound attributable to bitterns. Their calls have been either a coarse *gack-gack* given by birds on the nest or occasionally an *ank-ank* given by birds flushed in the marsh. However, it seems logical that the cooing call might be a courtship note given from the nest to attract females.

Copulation was witnessed at the nest twice during the present study. The first instance was two or more days after the nest was built and five or six days prior to egg-laying. In the second case, the nest held two eggs. Prior to copulation the male touched the back of the female's neck gently and preened her scapulars. Copulation on the nest during incubation is apparently common in the Little Bittern (Wackernagel, 1950; and Wijnaendts, 1954) and has also been observed in the European Bittern (*Botaurus stellaris*) by Yeates (1940).

TABLE 2

CLUTCH SIZE OF THE LEAST BITTERN (BASED ON INCUBATED OR FULL CLUTCHES)

Area	Authority	No. nests	No. eggs in clutch
Texas	Simmons (1915)	1	5
Ohio	Trautman (1940)	4	3
	Trautman (1940)	9	4
	Trautman (1940)	7	5
	Trautman (1940)	3	6
Iowa	Provost (1947)	1	4
	Provost (1947)	1	5
	Kent (1951, *in litt.*)	2	3
	Kent (1951, *in litt.*)	2	4
	Kent (1951, *in litt.*)	9	5
	Present Study	1	2
	Present Study	8	3
	Present Study	19	4
	Present Study	29	5
	Present Study	2	6
New Jersey	Potter (1917)	2	5
New York	Saunders (1926)	1	5
Ontario	Macoun and Macoun (1909)	1	5
	Macoun and Macoun (1909)	1	6
Wisconsin	Nero (1950)	1	5
Michigan	Baker (1940)	2	5
Minnesota	Roberts (1936)	4	4
Manitoba	Dillon (1959)	1	6
	Dillon (1959)	1	4
California	Moffitt (1939)	1	5
	Bancroft (1930)	1	5
	Willet and Jay (1911)	1	5
	Total	115	Mean = 4.48 ± .31

LAYING AND CLUTCH SIZE

The rate of egg-laying was reported by Trautman (1940) as one per day in four of six nests he observed. Others took slightly longer. In four nests I studied, the rate of laying was one egg per day in three nests, while another female required six days to lay five eggs. Incubation started with either the first or second egg, as indicated by embryonic development visible through a field candler. Incubation starts at the same time in the Little Bittern (Witherby, 1943:153).

A summary of data on clutch size is presented in Table 2. As far as possible, it includes only records of complete and incubated clutches. Even these records

TABLE 3

CLUTCH SIZE AND CHRONOLOGY OF NESTING*

Date	No. nests	Clutch Size Mean and S.D.**	Range
June 2–15	22	3.59 ± .67	2–5
June 16–30	28	4.89 ± .49	4–6
July 1–17	9	4.77 ± .25	4–5
	59	4.39 ± .43	2–6

*Based on 46 nests found during the present study and 13 nests located by Kent (**in litt.**) in 1951.

**Differences between means of early June and late June significant at the 99 per cent level; differences between means of late June and early July not significant.

could not be evaluated properly because laying rates were unknown or not stated in the paper. In at least two cases during this study, it was found that eggs damaged by predators were removed by the adults and incubation continued normally. Thus some small clutches reported in the literature may have been only part of a larger clutch. Four to five eggs are usual clutches in North America. Too few data are available to demonstrate latitudinal variation, but most clutches of six are reported from northern states. An even more interesting variation is suggested: of 46 complete clutches observed in this study, and 13 complete clutches found by Tom Kent in east-central Iowa (Kent, 1951, *in litt.*), all clutches found after mid-June—many of which may be renests or second nests—had four to six eggs; those found during early June had two to five eggs (Table 3). These differences are significant and demonstrate a pattern of seasonal change in clutch size which is the reverse of most double-brooded species (Lack, 1954:35), suggesting that the parents can feed more young in mid- than in early summer. A decline in clutch size in late summer is probable. This timing, as well as the late arrival and nesting of the species, probably is related to the chronology of available food organisms. Such a relationship has been shown for the Barn Owl (*Tyto alba*), which has a second and larger brood only when vole populations are high (Lack, 1954:35).

Also of interest for comparison is the clutch size of the Little Bittern (Table 4). While data are limited, it is apparent that clutch size of the European species is nearer six than five, as shown by both average and range. Clutches of eight have never been reported for the Least Bittern and clutches of seven are rare, but Witherby (1943:153) noted even larger clutches in the Little Bittern. He suggested that several females were laying in one nest.

Various workers have suggested that the Least Bittern rears two or three broods per season. No data from marked birds are available, but the chro-

TABLE 4

CLUTCH SIZE OF THE LITTLE BITTERN AS REPORTED IN THE LITERATURE

Area	Authority	No. nests	No. eggs in clutch
Germany	Groebbels (1935)	1	5
	Lucanus (1914)	1	7
Switzerland	Wackernagel (1950)	3	5
	Wackernagel (1950)	2	6
	Wackernagel (1950)	2	7
Holland	Wijnaendts (1954)	1	5
		10	5.8 Mean 5–7 Range
Less detailed; no. of nests not given:			
Germany	GroBkopf & Graszynski (1958)	–	7–8
	Steinfatt (1935)	–	5–6
Holland	Oort (1922)	–	5–7 (up to 8,9)
England	Witherby (1943: 153)	–	5–6 usual (also 4,7,8,9,10)

nology of nesting birds found during the present study suggests that two broods do occur (Fig. 2). These data undoubtedly are influenced by the varying intensity of nest hunting.

INCUBATION PERIOD

The incubation period of the Least Bittern has been determined as 15 days by Allen (1915), 16–17 days by Bent (1926), and 17 days by Bergtold (1917), but it was not clear from what point incubation was timed. Four nests observed in this study hatched in 19 to 20 days from the time of laying of the first egg (when incubation started) to the time when the first egg hatched. When timed by Heinroth's method (Nice, 1954) of counting from the laying of the last egg to the hatching of the last egg, incubation was 17–18 days in five nests. Using the same method, Baker (1940) reported a nest hatching in 18 days. Thus hatching requires only about three days while five to six days are required for laying the clutch.

Using Heinroth's method, data for the Least Bittern agree with that on Little Bitterns: GroBkopf and Graszynski (1948) reported 16.5 days, Oort (1922) found 17 days (range of 16–18 days), Groebbels (1935) reported 18–19 days, and Wackernagel (1950) approximately 19 days.

INCUBATION BEHAVIOR

Nest Maintenance and Incubation.—Incubation attentiveness is an extremely strong drive in bitterns. Chapman (1900), Allen (1915), Potter (1917), and Frost (1936) all reported birds which were so broody they could be

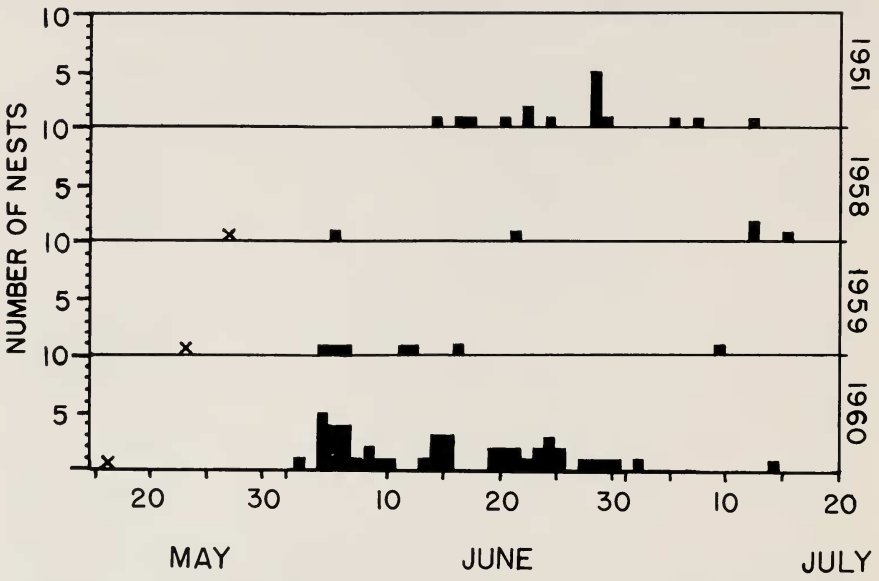

FIG. 2. Chronology of nest initiation in 1951 (Kent, *in litt.*) and 1958–1960 (present study). X = arrival of adults. Data calculated from either nest-initiation or hatching dates.

lifted from the nest. Two such birds were observed during this study. Wright (1946) found much individual variation among adult Least Bitterns which he studied, and Koenig (1953) reported similar variation among Little Bitterns and other European birds. During the incubation period, birds were never seen flying to the nest but landed in the nest area and approached the nest by quietly walking through the vegetation. Gabrielson (1914) reported that a clump of vegetation behind the nest was used as a landing site. The bird often hesitated at the edge of the nest to "roll" the eggs with the bill. Then it settled on the eggs by pushing the breast downward and rocking gently from side to side ("settling"). The posture maintained during incubation varies with the individual and the nest site. During long periods of incubation, the head is held low with the bill resting on the edge of the nest. The eyes are closed only occasionally.

Nest-building activities are few. Vegetation hanging over the nest is pulled down and worked into the nest. Continuous pulling of vegetation too strong to be pulled free results in a canopy. If the bird leaves the nest, it often returns with material which it adds to the structure. Or it may reach from the nest and pull material from the water. Experiments with artificial nests (see below) provided a source of material which was often utilized by the bird for its own nest.

TABLE 5

NEST BUILDING AND NEST JABBING IN RELATION TO STAGE OF THE NESTING CYCLE

	MALE		FEMALE	
	Minutes per poke or jab*	Observation time	Minutes per poke or jab*	Observation time
Incubation				
Nest 2 1958	—	None	30.0	6 hrs.
Nest 3 1958	12.0	6 hrs.	40.0	10 hrs.
Nest 1 1958	17.7	3 hrs., 50 min.	50.7	2 hrs., 32 min.
Nest 1 1959	20.9	5 hrs., 14 min.	29.5	3 hrs., 27 min.
Hatching				
Nest 1 1958	5.2	3 hrs., 48 min.	8.5	2 hrs., 50 min.
Nest 4 1958	10.9	2 hrs.	8.4	3 hrs., 30 min.

*This figure calculated from the number of "periods" of building activity, including "pulls," "pokes," or "jabs."

A nest-building action which appears more common than pulling of nest material—at least during the latter part of incubation—is "jabbing." With or without rolling the eggs with its lower mandible, the adult stares at the nest and jabs the bottom of the nest with either closed or open bill. This activity increases during the hatching period, but its exact function can only be hypothesized. Nest sanitation among the Ardeidae is commonly lacking (see Gross, 1923, on Black-crowned Night Heron, *Nycticorax nycticorax*; and Gabrielson, 1914, on the American Bittern), yet the Least Bittern uses a nest for nine days or more (Nero, 1950), and many nests remain exceptionally clean. Often a fragment of shell, a dragonfly wing or the feather sheaths of the young bird are the major evidences of nest use. Gabrielson (1914) noted one unsanitary bittern nest in river bulrush; a similar nest was found during the present study but was considered unusual. As with many young birds, defecation by juvenal Least Bitterns seems to be stimulated by the feeding of the parent and by handling. The fecal matter is of fluid mucous-like consistency. As the bird defecates, this fluid material flows over the nest material without clinging and flows through the holes in the nest. Possibly those holes formed by the "jabbing" activity of the parent assist in nest sanitation. Ryves (1946) considered sanitation as one of the possible functions of similar movements in passerines. Elimination of nest insects and aeration of the nest are other possible functions.

Table 5 summarizes nest-building activity such as pulling at vegetation, and jabbing the bill into the bottom of the nest. In three nests in which data were recorded during the incubation period, there were fewer periods of nest-building activity during incubation than during hatching. Also, it is apparent that the male performed nest-building movements more often than the female.

FIG. 3. Use of the wings in changing position on the nest.

Comfort Movements.—During long hours of incubation, turning is the most frequent movement. This is invariably accomplished with alternate opening and pushing with or refolding of the wings (Fig. 3). A quick rise and complete fluffing of feathers and shaking of the body is another common comfort movement. This may or may not be accompanied by preening, turning, poking, and settling. Partial shakes of either body or head also occur.

Gaping is common, especially following a period of alertness to food or intruders. A similar movement (Fig. 4) involves tongue stretching. Meyerriecks (*in litt.*) terms this "gagging" in the Green Heron (*Butorides virescens*). The

FIG. 4. Gagging.

Fig. 5. Preening.

bill is opened rapidly and more widely than in the threat posture. In one case, the gape was combined with a neck-stretch and wagging of the head and eventually the bird left the nest to drink, defecated, and returned to incubate. Another apparent fatigue-relaxing movement is the bill-stretch: the tips of the mandibles are held together but the mouth is opened proximally.

Irritations in the head region are scratched directly with one foot while balancing on the other. Body irritations are preened with a nibbling of the bill (Fig. 5). Extensive preening is usually started in the "ruff" of the lower neck—the powder-down area. Neck feathers are fluffed and individual feathers are preened with the bill tip from top to bottom. The mandibles are in slight but constant motion during the preening. The breast seems to be preened most often. Then the back of the lower neck, the belly, and flanks are preened but no definite order was noted. The greater primary coverts, primaries, and undercoverts are preened individually. There seems to be relatively little preening of the back. Feathers and other debris are removed from the bill by licking it with the tongue.

During warm periods, the head is held in any shady spot irrespective of the position of the body. Drinking is more common during warm periods and usually takes place a few feet from the nest. Panting is another means of cooling, and the "last resort" was seen in one case where the male left the nest, walked into water nearly three feet deep, and floated for a minute before returning to the nest and young.

After a rather long period of incubation, a female gave two calls not otherwise heard. The head feathers were fluffed, the head and bill were held vertically, and a *graa-wa-wa-wa* call given as the head and bill were returned

to their normal horizontal position. Later the same call was given but preceded by the *gack or quek,* which is a more common call given while on the nest.

Nest Relief Display.—Throughout incubation and brooding of the young, both sexes take turns on the nest. This change has a distinctive, though not elaborate, display. When one member of the pair comes to the nest, the incubating bird may ignore the oncomer, merely look alert, or assume a threat-like posture similar to that directed toward avian intruders. This seems to depend on the individual and the stage of the nesting cycle. The bird on the nest raises the crown feathers (these are also raised when drinking, leaving the nest, and with certain disturbances) and calls a low coarse *gra-a-a.* The oncoming bird, especially the male, has its crown and often its body feathers erect (Fig. 6a). When coming on the nest, both sexes shake their bills from side to side with the mandibles open, making a slight "rattling." At this time, the crown of the head is pointed toward the incubating bird and the bill points downward. This rattling seems very important in nest relief but also occurs when a lone bird of either sex returns to the nest after drinking. This posture was observed during incubation and brooding. Gabrielson (1914) described this action and noted a male doing this for fully 10 minutes before the female stepped from the nest and flew away. I have never observed a delay of this length, but one female refused to leave despite the fact that the male rattled for nearly five minutes. The male left and returned a short time later and repeated his performance. He finally entered the nest, whereupon the female departed. In this case, as in Gabrielson's study, there were young in the nest. At other times, the bird on the nest rarely hesitated. Usually, the bird on the nest also erects its crown feathers and stands. The oncoming bird depresses its crown feathers and assumes a posture with head lower than the standing bird (Fig. 6b). The air is one of cautiousness; at this time the necks may be crossed and the bill occasionally touches the back of the neck (Fig. 6b). The incubating bird then leaves (Fig. 6c), often taking flight from a nearby clump of vegetation.

On some occasions, the male of one pair placed a bulrush stem in the nest—but did not give it to the female as noted by Potter (1917). On another occasion, a female brought a stick of vegetation to the nest while the male was on the nest. Occasionally, sticks were brought back to the nest when birds of either sex left for food or drink. This type of behavior may be the forerunner of the more elaborate nest-relief behavior of other herons involving transfer of nest material.

Incubation by both sexes with a nest-relief display seems important to the strength of the nest attachment and to the maintenance of constant nest attentiveness. I never witnessed a bird leave a nest (under normal conditions)

Fig. 6a. (Top) Male approaching nest with crown and body feathers erected. Female has crown depressed.

Fig. 6b. (Bottom) Submissive attitude of female as she enters nest.

without first undergoing the nest-relief ceremony and having the mate take its place. When birds were flushed from the nest, the bird of the same sex always returned. Birds of either sex left to catch food, drink, or gather nest material but always returned within a minute and were not out of view of the nest. However, it appears that when both sexes are near the nest, the mate not on the nest will take over if one bird is frightened away.

Whether this display is truly vital to any change-over at the nest is uncertain. In an attempt to evaluate this, a stuffed male bird was placed on the nest. If the female returned, would she ignore a male which incubated rather than

FIG. 6c. Male's crest erected as female departs. Note her depressed crown feathers.

displayed? In two of the three trials on two different nests, males returned. Oncoming birds of both sexes approached cautiously, with typical erect crest and body feathers, and came on the nest despite the presence of the dummy. In all cases, they approached from behind the bird, hissed, and pecked it at the back of the head. To prevent desertion of the nest and damage to the skin, the incubating bird then was flushed from the nest.

Comparative Attentiveness of the Sexes.—The unique sexual dimorphism among the members of the genus *Ixobrychus* allows easy determination of relative attentiveness of the sexes in incubation. Groebbels (1935) presented data on one nest of *I. minutus*: in 14 hours and 35 minutes of observation, the female incubated the eggs 9 hours and 33 minutes while the male attended the nest only 5 hours and 2 minutes. Observations at five nests during this study totaled 54 hours and 39 minutes. During this time, the females incubated 32 hours and 35 minutes (59 per cent), while the males incubated only 22 hours and 4 minutes. Although there is a great deal of chance involved in which bird is on the nest when the observer is present, the length of the observations suggest that the female does most of the incubating. The longest period of incubation observed was by a female which incubated for five hours. During this time she left the nest briefly when frightened by the observer and then briefly when the observer left the blind. After an hour away from the nest, the investigator returned to find the female still incubating. Two additional hours of observation showed that the female incubated at least seven of the eight hours of observation. Several males incubated at least three hours, but longer observations were not available. Females did more feeding and drinking at the nest, presumably because they incubated for longer periods.

FIG. 7. Male watching food below nest.

Experiments with Artificial Eggs and Nests.—Experiments with artificial eggs and nests were attempted (1) to determine whether the sight of exposed eggs would stimulate incubation behavior despite the fact that the eggs were not in the proper nests, and (2) to learn whether both birds would incubate simultaneously if two nests were provided. In neither of two attempts did both birds appear. Nevertheless, birds of both sexes presented with artificial nests were much interested in them. One used the nest material for construction of its own nest. The rough-textured balsa eggs used in the first experiment apparently were not adequate to induce incubation but produced some interesting results. The balsa eggs were placed in the real nest and the real eggs were placed in the artificial nest. The male returned and immediately removed three of the balsa eggs and started over to the artificial nest. Then he returned to the real nest but obviously was not comfortable and finally left. The female came on immediately and without hesitation dropped out or carried away the two remaining artificial eggs; then she incubated on the empty nest, in full view of the artificial nest containing the real eggs. Apparently the nest is a stronger attraction than the displaced eggs when the nest is a conspicuous structure. Allen and Mangels (1940) reported similar behavior in Black-crowned Night Herons. Among species such as gulls which can easily roll their eggs into the nest, Tinbergen (1953) found that Herring Gulls usually preferred the eggs to the nest site but this depended on the local terrain.

Food Consumed.—During the intensive observation at nests, three females and two males were observed to feed while incubating. All birds spent considerable time observing the movements of prey items in the water below. When food is near, the crest and body feathers may be erected (Fig. 7) and

TABLE 6

FOOD ITEMS REPORTED IN THE LITERATURE

Authority	Number of birds	Foods
Adults		
Eifrig (1915)	1	2 sunfish
Gosse (1847)	–	small fish and crustacea
Roberts (1936)	2	crayfish (pincers removed) and snails
Saunders (1926)	–	small fish and arthropods
Simpson (1939)	7	small fish, insects, frogs, mammal
Wetmore (*in* Howell, 1932)	93	40% fish, 21% dragonflies, 12% insects, 10% crayfish, 18% miscellaneous
Young		
Gabrielson (1914)	–	frogs
Nero (1950)	–	minnows

gaping is common. Food which came within reach of the incubating birds made up most of the prey items, but the bird got off the nest and went to the water for prey for six of 34 observed feedings. Items taken were: five unidentified items, probably frog tadpoles; six unidentified insects; one grasshopper; 21 damselflies; and one tadpole. In addition, a male was observed feeding frog legs to the young. Despite the fact that snails were common around the nest, they were never eaten. However, Roberts (1936) reported snails in the stomachs of two specimens he examined. Success in capturing previously-spotted prey appeared to be nearly 100 per cent. There are relatively few data on food habits (summarized in Table 6).

Reaction of Adults to Potential Predators.—Chapman (1900) saw a Long-billed Marsh Wren (*Telmatodytes palustris*) pierce the eggs in a bittern nest; he regarded this as interspecific territory dispute. Common Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), and blackbirds may take eggs for food. Damage to only one egg in the nest does not always cause desertion; damaged eggs are removed and nesting continues normally. Marsh wrens, blackbirds, and Black Terns (*Chlidonias niger*) are often threatened by incubating birds by depressing the crown and withdrawing the neck preparatory to striking. Crown feathers may be raised and lowered when intruding birds are at a distance. When near, the bill is held open and a *gra-a-a* call may be given. The most intense aggressive posture involves withdrawing the head and spreading the wings with their dorsal surfaces facing forward. This posture is directed toward men (Chapman, 1900; Allen, 1915) and occasionally is assumed at wrens.

FIG. 8. (Left) Freezing behavior at the approach of a Great Blue Heron.
FIG. 9. (Right) Female removing egg shell from the nest.

Two observations were made during the present study which suggest behavior toward large predators. In one, a female suddenly rose from the normal incubation posture to the "freeze" (Fig. 8), and a Great Blue Heron (*Ardea herodias*) flapped over. The same female and another were observed watching buteos which were soaring at such heights that they could not be identified by the observer. That buteos may prey on bitterns was assumed when a young Red-tailed Hawk (*Buteo jamaicensis*) was found standing in water on a weak but live adult female bittern.

Predators on young probably include turtles, as Trautman (1940) saw one take an adult. During this study, several dead and partly eaten young bitterns were found in the water near a nest. The absence of fish in the lake implied that turtles were responsible. A garter snake (*Thamnophis ordinatus*) was observed which was attracted to young bitterns, but Kent (1951) saw a water snake (*Natrix sipedon*) pass directly over a nest without attacking the young.

HATCHING SUCCESS

Of 38 nests observed for hatching data, at least one egg hatched in 32 (84 per cent). Average clutch size of this group was 4.0, and averages of 3.5 young were reared per successful nest and 3.0 for all nests observed. These

success data are believed to be biased upward by the fact that most nest loss occurs during the first few days of laying and building when eggs are more likely to be exposed. Few nests were found in this early stage but many empty nests were located which probably had been deserted. Because these nests could not properly be evaluated, only nests with complete histories were used for success data.

CARE OF THE YOUNG

Behavior of Adults During Hatching and Rearing.—During hatching and rearing, the adults seem more hesitant to leave the nest. Nest relief displays by the oncoming bird are more intense and of longer duration. When the brooding bird finally leaves, it may stay away for only a short time. Hatching is often observed closely by the adult and as soon as the young are free from the shells, these are carried away (Fig 9) and dropped in the water or eaten.

After the young are free of the shell and before they are dry, they are fed by regurgitation. Apparently, the adult's bill must be lowered to the young before feeding occurs. If hungry, the young grab the bill violently (see Bates, 1943, for a description of this in the Little Bittern). However, the bill may be raised again if the adult is not ready to feed. The stimulus causing feeding response in adults is not clear. The adults seem to feed only if the young are active. The young open the bill in a fashion similar to the gaping of passerines but this does not seem regular. "Peeping" calls by the young seem more prevalent when they are hungry and may serve as the releaser. Or, the bill of the young may be a stimulus when it is held vertically (as when hungry) but not when held horizontally or slanted so that the down of the head hides the bill from view.

Gabrielson (1914) noted that all young in a nest were fed at each feeding, but Davidson's (1944) data indicated that this varied. In general, feeding of young occurs only when the young grab the bill—again suggesting that food is only regurgitated by a sign stimulus from the young—and therefore the number of young fed depends on their desire to feed. Gabrielson found that the young were fed only four times in one day, and Davidson's (1944) data also suggested a limited feeding schedule. During the present study, only two of the five nests were observed for a significant period after hatching. During 11 hours and 54 minutes of observation on two of these nests, females were on the nests 6 hours and 6 minutes and males brooded 5 hours and 48 minutes. During this time, females attempted to feed some or all young once every 20 minutes while males fed every 10 minutes. This agrees with statements by Gabrielson (1914) and by Breckenridge (*in* Roberts, 1936:194) that the male does most of the feeding. However, the rate of feeding undoubtedly varies with the age of the young and the nature of the food.

Young may be shaded by an adult standing over them (Fig. 10).

FIG. 10. Shading of young and panting and sunning by the male.

Innate Responses of the Young.—When just free from the shell and still wet, the young bittern is equipped with those reflexes vital to its survival. The gripping response of the feet is weak but apparent whenever the bird is moved or its feet are removed from a solid surface. If turned on its back or side, it attempts to right itself by swinging its feet and grasping. When held on an inclined plane, the feet push forward and prevent the bird from slipping. The bird is nearly able to hold itself on a branch when newly hatched and birds one day old or more certainly can keep from falling from the nest by this means. At several days of age, the bird can firmly grip twigs and remain in that posture for some time (see Nero, 1950). When gripping a piece of vegetation, the bird uses its wings and curved neck as well as its feet and counterbalances the body with the head.

The eyes are closed for nearly ten minutes after the bird leaves the shell and it does not respond to artificial bills for about 35 minutes. At that time. it can hold its head up for only a few seconds. Two moves are apparent within 15–20 minutes after hatching; the bill is opened in a quick gape-like movement but is not held open as in passerines. Also, the base of the bill is stretched as in adults. The ability to hold up the head possibly is vital to survival for the adult is probably stimulated to feed by the raised head of a hungry bird. The juvenile is attracted as soon as the adult's bill is placed before it. It feebly moves the bill toward the adult's bill and turns its head

in order to grip the adult's bill. The regurgitated food then passes down the adult's bill and commonly strikes that of the juvenile. As the juvenile's mandibles follow the food down to the tip of the adult's bill, the food is easily taken. In this fashion, the young also are directed to food which may fall into the nest and the young quickly learn to recover this. During early feedings, the adults recover any food dropped into the nest. On one occasion, two young of three or four days of age were competing for a pair of hind legs of a frog. This invariably resulted in each getting one of the two legs and a tug-of-war ensued so that the legs fell to the bottom of the nest. The small size of the young and the large size of the legs prevented recovery by the juveniles. The male reswallowed and regurgitated this pair of legs eight times and the result was always the same! The legs were still not consumed when I was forced to leave the blind.

As the young reach about three days of age, they respond to any non-bittern form by "freezing." At five to seven days, they assume the aggressive posture with the neck down, the head ready to strike, and the wings held open with their dorsal surfaces facing forward. Portielje (*in* Tinbergen, 1953:214) showed that a distinct head shape was essential in models to release the striking attack of European Bitterns. During this posture, young Least Bitterns sway back and forth from side to side. This behavior is common in adult American and Least Bitterns and reportedly occurs as a camouflaging mechanism when marsh vegetation is moved in the wind (Saunders, 1926). However, Elliott (1951) reported this behavior in a captive Least Bittern indoors. At six to nine days, the young leave the nest, apparently to seek shade and possibly to feed as well. They move through the reeds with great skill but occasionally get wet in doing so. Their color is light tan, common to the young of many marsh birds, and they are well camouflaged in the nest and in old vegetation. They return to the nest when the adult comes to feed them. Whether or not the adults feed the young in the vegetation is not known. Nero (1950) had to fence birds to keep them at the nest but also found banded young in the area of the nest at 27 days of age (Nero, 1951).

Experimental Analysis of Feeding Responses of Juveniles.—That the adult's bill is the stimulus for feeding behavior in juveniles and that there is a simple innate response in juveniles is indicated from tests with model bills. A yellow pencil was sufficient stimulus for some birds, and one juvenile of six to seven days of age grabbed the yellow leg of the male and tried to feed! Unfortunately, too few young were available to test all newly hatched young without the influence of learning and to make tests statistically significant. Nevertheless, they indicate an instinctive feeding response.

Models of flat cardboard and three-dimensional models of cardboard and wood were used. There was no difference apparent, but three-dimensional

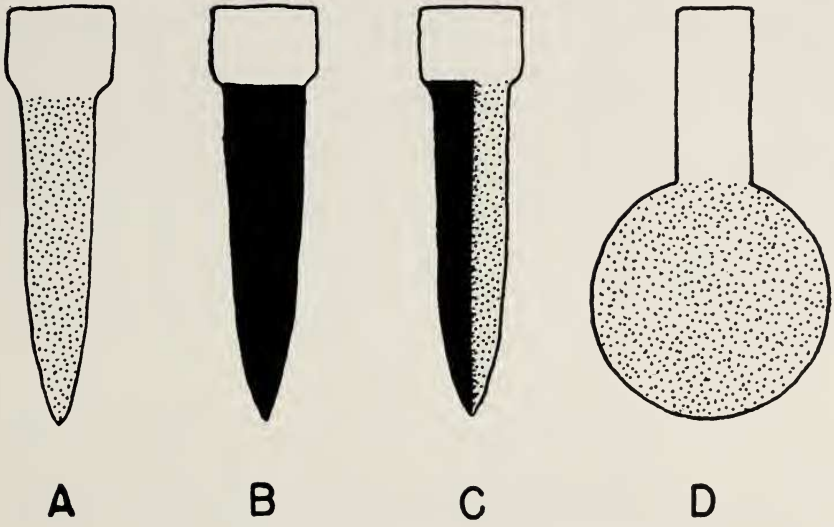

Fig. 11. Models used to test feeding responses of young.
A = yellow or gray; B = black; C = black and yellow; D = yellow or gray.

models of wood were selected for use in the field because of their durability. These were painted gray, black, yellow, and yellow and black (Fig. 11). In testing, the bill was held vertically in front of a bird and moved up and down gently for five seconds. The response was recorded as positive or negative, although several grabs at the bill often were made during that period. Most tests were performed on birds of one to four days of age although aggressiveness at the latter age occasionally voided results. Some birds were sleepy and could not be awakened; others were not stimulated by the bill and probably had just been fed by the parents. Those tests which produced some positive results are summarized in Table 7 and show that any elongate object may produce a grabbing response. The effectiveness of gray was surprising and stresses the value of an elongate form as part of the releasing mechanism. To test the significance of color, gray cardboard was cut in a circular form (Fig. 11) and painted yellow on one side. In tests, the yellow stimulated a feeble pecking (not grabbing as with bill models) but gray resulted in no response. Thus, color as well as form is part of the releaser which causes feeding behavior. When birds were presented the cardboard circles, it is of interest that very little effort was made to turn the head, and pecking was directed at the edge. Similar tests with a square model provided similar results but with greater tendency to turn the head parallel to the edge of the model. The importance of parallel positioning of juvenile and adult bills as a second step in releasing feeding response was tested by presenting artificial

Table 7

Response of Young Birds to Artificial Bills

(number of positive responses over number of tests)

Age of young	Gray	Black	Yellow	Black and Yellow	No. of Individuals
Newly hatched*	0/6	0/6	6/6	4/5	6
1–4 days	11/16	10/31	25/31	28/30	16
Totals	11/22	10/37	31/37	32/35	22

*At least two of these had never been fed by the parents.

bills to young in a horizontal position. A positive response resulted in 8 of 13 trials.

Based on present limited data, the response of young birds seems to be a two-step reaction. The elongate form and yellow color stimulate an initial reaction. Secondly, the juvenile presumably aligns its normal line of vision so that the adult's bill is horizontal. Both sexes have a reddish base to the bill and this is brighter in the male than in the female (and the male does most of the feeding), but the significance of this red area as a releaser was not tested experimentally.

SUMMARY

The nesting behavior and habitat of Least Bitterns was studied in several glacial lakes and marshes in Iowa. Eighty-nine nests were found, and intensive observations from blinds were made at five nests. Nests were mainly in *Typha* spp., *Scirpus acutus*, and *Scirpus fluviatilis*. Clutch size varied from two to six eggs with the smaller clutches being found early in the season. Copulation occurs on the nest during early incubation and possibly there prior to incubation. Incubation required about 19 days from the laying of the first egg to hatching of the first egg and 16–17 days from the laying of the last egg to the hatching of that egg. The species appears to be double-brooded in Iowa, at least in some years.

Nest incubation movements are: bringing material to the nest, pulling in material from above, and bill-jabbing in the nest bottom. During incubation, the bird rolls the eggs with the lower mandible, settles on the eggs by a rocking motion, and remains alert during even long periods of incubation. Comfort movements were shaking, turning, gaping, scratching, preening, drinking, and panting. Both sexes incubate, and nest relief includes a simple display of erecting the crown and body feathers, "rattling" of the bill, and

occasional crossing of bills or touching of bill to back. The oncoming bird slips under the incubating bird. During nearly 55 hours of observation, the female incubated 59 per cent of the time. Incubating adults fed on passing damselflies and other insects, and occasionally left the nest to take nearby prey. Wrens, blackbirds, hawks, snakes, and turtles are thought to prey on eggs, young, or adult bitterns.

During hatching, adults remove the egg shells or eat them. Both sexes feed the young by regurgitation but the male feeds more often than does the female. Innate responses of the young which are considered important to survival are gripping of the feet, holding vegetation with the wings, and balancing with the head. The stimulus for feeding in young probably is a yellow-colored and elongate structure. These releasers were tested briefly experimentally. The releaser for parental feeding behavior is unknown but is probably the sight of raised bill of the juvenile.

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